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INTERANNUAL VARIABILITY IN DOLPHIN HABITATS IN THE EASTERN TROPICAL PACIFIC, 1986-1989

By

S.B. Reilly and P.C. Fiedler

ADMINISTRATIVE REPORT LJ-90-29

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IN THE EASTERN TROPICAL PACIFIC, 1986-1989**

November 1990

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INTRODUCTION

The eastern tropical Pacific (ETP) supports a cetacean fauna that is both diverse and abundant, including over 25 species (Au & Perryman 1985, Leatherwood et al. 1982). It is a vast area, larger than the entire North Atlantic. Its waters are truly pelagic, except near a few islands and over a narrow continental shelf. Prior to the 1960's almost nothing was known of the distribution and ecology of the region's cetaceans beyond the summaries of catch localities from 19th Century fisheries for large whales (Townsend 1935).

By the late 1960's, it became clear that large numbers of dolphins were being killed in the ETP in tuna purse seine operations (Perrin 1969). The US government initiated a program at that time to place scientific observers on purse seiners to monitor dolphin mortality (Smith 1983). Beginning in 1974, research vessels were dispatched to the region to supplement the observer data (Holt et al 1987). The combination of these efforts has produced unprecedented amounts of information on pelagic cetaceans.

In this study we focused on the dolphin species affected by the tuna fishery: spotted dolphins (Stenella attenuata), spinner dolphins (S. longirostris) in two morphological forms, "whitebelly" and "eastern" (Perrin 1989), striped dolphins (S. coeruleoalba) and common dolphins (Delphinus delphis). We included other cetacean species to allow community-level interpretation of habitats and their variability.

Dolphin distribution patterns have been described from the sighting and collection localities (e.g., Au & Perryman 1985, Evans 1975, Perrin 1975, Perrin et al. 1983). Au & Perryman (1985) studied cetacean habitats of the eastern tropical Pacific from sightings and oceanographic data collected during the northern winter. They described two complementary patterns for the smaller cetaceans, both with apparent links to the region's oceanography. One pattern, shown by common and striped dolphins, coincided with "upwelling-modified" conditions, found along the equator, and at the tropical terminations of eastern boundary currents off Baja

California and the coast of Ecuador and northern Peru (described in more detail below in Study Area). The second pattern, shown by spotted and spinner dolphins, coincided with largely tropical waters off Mexico, where warm, low-salinity surface waters occur over a strong, relatively shallow thermocline.

Reilly (1990) examined ETP dolphin distributions in the northern summer, and quantitatively tested Au & Perryman's habitat hypotheses. He found an apparent offshore shift in spotted, spinner and striped (but not common) dolphins coincident with seasonal shoaling of a thermocline ridge along 10 N (Fig. 1). This seasonal shoaling is part of the dominant pattern of seasonal change in the ETP, associated with the north-south movement of the Intertropical Convergence Zone between the trade winds (Fiedler 1990). Statistical tests supported the habitat hypotheses of Au & Perryman (1985) for spotted, spinner and common dolphins, but not for striped dolphins. In the summer striped dolphins occupied habitat that was geographically complementary with both that of common and of spotted/spinner dolphins (Fig. 1). Striped dolphin habitat was not statistically distinguishable from either the upwelling-modified or tropical habitats with the variables used, indicating that other factors or processes act to separate these dolphins from the others.

Interannual variation in the region's oceanography is dominated by the quasi-periodic El Niño-Southern Oscillation (ENSO; Enfield 1989). Interannual variation exceeds seasonal variation in most of the ETP (Fiedler 1990). ENSO variability affects all of the patterns and processes so far identified with cetacean habitats. From this we hypothesized that cetacean distributions might change interannually in response to changes in the distribution of their habitats. If so, this could have important implications for the monitoring of trends in the animals' abundance now in progress from both research vessel surveys (Gerrodette & Wade 1990) and tuna vessel observer data (Anganuzzi and Buckland 1989).

The primary objective of this study was to examine interannual variability in cetacean habitats, defined by the most appropriate available multivariate techniques, for the years 1986 - 1989. We also suggest methods to use habitat information in the monitoring of trends in cetacean abundance. That is, given a quantitative definition of habitat and a record of interannual changes in habitat distribution, can we reduce variance and/or bias in the trend monitoring?

STUDY AREA

The basic physical features of the upper ocean in the eastern tropical Pacific have been described by Wyrtki (1966, 1967), and Tsuchiya (1974). Fiedler (1991) updated this description and summarized seasonal and interannual variability. Major surface water masses and currents are depicted in Figure 2.

Warm, low-salinity Tropical Surface Water is found in the center of the ETP. Cooler, higher-salinity Equatorial Surface Water is found south of about 3N. Peru Current and California Current Waters are found along the coasts of Peru-Ecuador and Baja California, respectively. The Peru and California Currents feed into the westward South and North Equatorial Currents (SEC, NEC). The North Equatorial Countercurrent (NECC) flows eastward between the NEC and SEC into the center of the Tropical Surface Water mass. The NECC is strong in September-December and weak or absent in February-April.

A permanent, shallow thermocline underlies most of the region, shoaling towards the coast (Wyrтки 1966). Zonal thermocline ridges are found below surface divergences in the SEC along the equator and between the NEC and NECC along 10N (Fiedler 1991). Upwelling driven by equatorward longshore winds off Peru and Baja California and by trade winds along the equator brings cold, nutrient-rich water from below the shallow thermocline (nutricline) into the surface layer. This nutrient input maintains optimal (saturating) concentrations of new nitrogen at the surface and results in high levels of new production in equatorial and eastern boundary current systems (Chavez and Barber 1987). Biological productivity is also enhanced by upwelling at the Costa Rica Dome (a quasi-permanent cyclonic eddy at the eastern end of the thermocline ridge along 10N; Wyrтки 1964, King 1986), and by intermittent, topographically-induced offshore winds at several points along the coast of Central America (e.g. the Gulf of Tehuantepec, McCreary et al. 1989).

Secondary and higher level productivity and standing stocks are generally high in areas of high primary productivity (Blackburn et al. 1970). Within this and other large oceanic regions, the abundance of animals from plankton to large nekton is patchy on a variety of spatial and temporal scales (Haury et al. 1978), with major consequences for the ecology of pelagic predators (e.g., Carr 1987).

DATA & METHODS

Field Data Collection.

Both cetacean sightings and oceanographic data were collected by two ships operating in different parts of the ETP from July 28 through December 6 each year from 1986 - 1989 (Holt et al. 1987). Track lines are shown in Fig. 3. The surveys were conducted at 10 knots (18.5 km/hr) with three observers simultaneously on watch, one covering each side of the ship with a pair of 25x ship's binoculars to search an arc from the ship's bow to about 100° to the beam. The third observer covered the track line with hand-held binoculars and the naked eye. Sightings were approached when necessary to allow estimation of numbers within groups and species identification (Holt & Sexton 1990).

While the ships were underway, surface temperature and salinity were recorded continuously by thermosalinograph (ODEC Model TSG-102, Inter-Ocean Model 541 or Seabird SEACAT Model 21). Vertical structure was sampled in two ways. XBTs were deployed 4 to 6 times daily (every 55 to 110 km). Twice daily, just before dawn and just after dusk, the ships stopped to deploy CTDs to 1000 m. Sea water samples were collected with Niskin rosettes for chlorophyll and nutrient analysis. Surface chlorophyll was monitored continuously with a Turner Designs Fluorometer calibrated from discrete samples drawn at the surface at least six times per day (see Fiedler et al. 1990 for more detail).

Analytic Methods.

We estimated cetacean abundance, as the number of pods sighted per distance searched, for each day for 16 species or stock categories (Table 1). Only days with at least two hours of sighting effort (approximately 37 km) during periods of good sighting conditions (Beaufort 5 or less) were used in the analyses. The distance searched in one day varied between 37 and 222 km. We analyzed each day's sightings in relation to environmental conditions measured during that day.

Reilly (1990) found that dolphin habitats in the ETP could be statistically defined by a combination of thermocline depth, surface temperature and salinity (combined into sigma-t). We used these variables plus an estimate of surface chlorophyll, log-transformed. Surface temperature, salinity and chlorophyll were averaged from the day's continuous sampling during sighting effort. Thermocline depth was represented by the depth of the 20°C isotherm (Donguy & Meyers 1987), averaged from XBT casts during or within a few hours of sighting effort. The four environmental variables (surface temperature, TEMP; surface salinity, SAL; thermocline depth, Z20; chlorophyll, LOGC) were normalized prior to multivariate analyses to remove effects from differing scales of measurement.

The relationships between cetacean species distributions, community structure and environmental variation were analyzed using canonical correspondence analysis (CCA; Ter Braak 1986). We used the computer program CANOCO (Ter Braak 1985). Correspondence analysis is an eigenvector ordination technique, used similarly to principal components analysis to determine community structure. These methods extract dominant, orthogonal axes of variation in abundance indices for multiple species at multiple sites. Typically, the ordination axes are then interpreted indirectly with the help of external knowledge and data on environmental gradients, either qualitatively or with regression methods (Gauch 1982).

In contrast to PCA and other so-called "linear" methods,

correspondence analysis (CA, also called reciprocal averaging) fits non-linear Gaussian (unimodal) models to the species abundance data. Canonical correspondence analysis is an extension of CA in which the species ordination is done directly and iteratively in relation to environmental variables. CCA is an efficient ordination technique when species have bell-shaped response curves or surfaces with respect to environmental gradients (Ter Braak 1986), which is consistent with general ecological knowledge (e.g. Whittaker et al. 1973). The models and algorithm used in CCA are summarized in the Appendix.

As part of the species-environment ordination, CCA estimates a series of site scores (here, site = day) that are linear combinations of the environmental variables that maximize the species-environment correlation. One set of site scores is estimated for each canonical ordination axis. The interpretation of environmental patterns represented by the axes is made from the multiple regression or "canonical" coefficients of the original variables on the canonical axes, and the correlation coefficients between the original environmental variables and the ordination axes (Ter Braak 1986).

The results of canonical correspondence can be best interpreted from an ordination "biplot", on which species and sites can be represented by points and environmental variables by arrows. The biplot displays the site-weighted mean species scores or "optima" on two canonical axes, usually the first two, which explain the majority of the variance. The directions and relative lengths of the arrows for environmental variables represent their contributions to the ordination. Important environmental variables are therefore represented by longer arrows than variables of lesser importance.

Community ordination was not our primary focus, but we used CCA for three reasons. It provides a quantitative definition of habitat for each species/stock in reduced dimensionality. The method estimates habitats using a non-linear, unimodal model, avoiding the unrealistic assumption of a linear relationship between animal abundance and environmental gradients. CANOCO is also insensitive to a high frequency of zero observations (Ter Braak 1985), typically found in animal survey data.

We conducted the analysis with data from all years combined to estimate general patterns. We then removed the variance associated with the environmental variables (by defining them as covariables) and extracted axes associated with variance among years, to test for interannual differences in the species data not associated directly with interannual environmental variation.

The validity of an ordination axis was determined by testing the null hypothesis that its eigenvalue was not different from zero. The procedure used was a Monte Carlo randomization test

(e.g., Hope 1968) supplied with the program CANOCO. This procedure randomly associated sets of environmental variables from one case with sets of species data from another, extracted axes, estimated eigenvalues, etc. The procedure was run 100 times to produce a reference set of eigenvalues representing random variability. The significance of the eigenvalues from the original data was determined by comparison to these distributions.

We extended the use of canonical correspondence analysis in two ways in our study of interannual variation in cetacean habitats. First, we mapped the spatial distributions of the site scores from the first two CCA axes, lightly smoothed and contoured. We then plotted the localities of cetacean sightings over these contours to allow visual appraisal of species-environment patterns. We did this as an alternative to plotting species and hundreds of sites together on a biplot, which we found to be uninformative.

Second, we suggest two ways in which the results of the canonical correspondence analysis can be used in the monitoring of trends in cetacean abundance.

RESULTS

The research vessels searched a total of 118,907 km, and recorded a total of 3,136 cetacean sightings during 1986 - 1989 (Table 1). The environmental data used include continuous temperature, salinity and fluorescence measurements along most of the trackline, 12,855 surface chlorophyll measurements, 3,917 XBTs and 1,228 CTDs (Table 2).

Table 3 gives the weighted correlation matrix for the original environmental variables, the four species axes and four environmental axes from the CCA. The "species-environment" correlations are the values for equivalent axes, e.g., the correlation between the dominant species axis (no. 1) and the first environmental axis is 0.64. The correlation between the second axes is 0.45, and so on.

The eigenvalues for the ordination axes indicate that only the first two are important (Table 4). Axes 3 & 4 together represent only 8% of the variation of the species - environment data. Ter Braak (1985) suggests that eigenvalues less than 0.02 be disregarded. The first axis accounts for 67% of the variance extracted, the second accounts for 25%, together they represent 92%. Further results and discussion therefore relate to only axes 1 & 2.

The relationships between most of the species categories of interest and the first two environmental axes were unimodal (Fig. 4), satisfying a primary assumption of CCA. One exception was common dolphins on axis 1, where there is strong evidence of

bimodality.

A Monte Carlo randomization test resulted in rejection of the null hypothesis of no relationship between the species encounter rates and the environmental data ($H_0: \lambda=0$). One hundred random permutations produced no extractions with a trace (eigenvalue total) larger than the observed .301 (the largest random trace was .197), giving a P-value $< .01$. Likewise for the first axis alone, no random permutation had an eigenvalue larger than the observed .201, the largest being .042, again giving a P-value $< .01$. These results indicate that the probability of a Type I error is less than 1%. (The CCA program, CANOCO, provided this test only for the trace and first axis, so no test was done for subsequent axes).

All significant interannual variation was accounted for in the environmental data. After extracting variance in the species data related to the environmental variables (by treating them as covariables) the eigenvalues associated with inter-annual variation totaled just .03. This eigenvalue trace is not significantly different from zero (Monte Carlo $P = .21$). The residual variance in the species data, i.e. variation not related to the environmental variables included here, had an eigenvalue of 0.42. The approximate " R^2 " or proportion of the total variance accounted for in the CCA was therefore $.30/ (.30 + .42) = .42$, or 42% (Table 4).

The species-environment biplot (Fig. 5a) displays the ordination results. Figure 5b shows the ordination with error bars on selected species/stocks, without the visual distraction of the environmental vectors. The first axis separates common dolphins from spotted and spinner dolphins of all categories. Positive scores on axis 1 are associated with cool temperature ($r = -0.93$, Table 3), shallow thermocline (small Z20, $r = -0.54$), and high chlorophyll ($r = +0.49$). We interpret these as characteristics of a "cool upwelling" habitat, as found in Equatorial and Peru/California Current Surface Waters. This is the preferred habitat of common dolphins. Negative scores on axis 1 are associated with warm temperature, a deeper thermocline, and low chlorophyll, as in less productive Tropical Surface Water.

Site or species scores on axis 2 are uncorrelated with scores on axis 1, by definition. Positive axis 2 scores are associated with a very shallow thermocline ($r = -0.81$, Table 3) and high chlorophyll ($r = +0.40$) as for axis 1, but also with low salinity ($r = -0.32$) rather than cool temperature. We interpret these as characteristics of a "coastal tropical" habitat found along the coast of Central America, where the surface layer is more stratified and upwelling is more intermittent and localized than in the "cool upwelling" habitat.

Whitebelly spinners, alone and with spotted dolphins, had large positive axis 2 scores, while eastern spinners with spotted dolphins had negative scores. There was thus a strong separation

on axis 2 between mixed schools of spotted dolphins with whitebelly and eastern spinners. Eastern spinners alone and spotted dolphins alone had near-zero axis 2 scores. Blue and Bryde's whales are also distinctly separated on this axis. Blue whales had the lowest axis 2 scores (strongest association with "coastal tropical" habitat) of any species/stock.

A number of species loaded near the origin of both axes, including striped dolphins, sperm whales, Risso's dolphins and pilot whales. This indicates either that this is near the "optimum" habitat for these species, or that their distributions are unrelated to the axes. The large error bars for striped dolphins (Fig. 4b), and their spatial distribution (below) support the latter interpretation.

The spatial distributions of yearly axis 1 scores are mapped in Figure 6. "Cool upwelling" habitat (positive scores) is shaded to allow quick appraisal of changes between years. In 1986, "cool upwelling" habitat was found across the study area south of 0-5N to the coast between Costa Rica and Peru and off the coast of Baja California. In 1987, "cool upwelling" habitat did not extend west of 110W or north of 3N, except in the Gulf of Panama. The study area was dominated by warm, low-productivity tropical water (negative axis 1 scores). This change was caused by a moderate El Niño event that began in late 1986 and lasted through 1987 (Kousky and Leetmaa 1989). In 1988, "cool upwelling" water extended far north of the equator and south of Baja California, considerably reducing the area covered by tropical water. 1988 was a strong anti-El Niño or La Niña year (Leetmaa 1990, Fiedler et al. 1991). In 1989, conditions represented by axis 1 scores returned to a state similar to 1986.

Also plotted in Fig. 6 are sighting localities for spotted and common dolphins. Spotted dolphins occurred mostly in negative areas, common dolphins in positive areas, but with some overlap. In 1987, with "cool upwelling" conditions contracted eastward and southward at the equator, common dolphins occurred in the southern ETP only in the far east off South America. In 1988 when these conditions were strongly established along the equator to the western extent of the study area, common dolphins occurred in equatorial waters as far west as 110W.

Spatial distributions of yearly axis 2 scores are mapped in Figure 7, with "coastal tropical" habitat shaded. "Coastal tropical" habitat overlaps "cool upwelling" habitat in eastern equatorial water and also is found in small patches along 10N in the western part of the study area. Interannual variation along this axis is not as strongly related to ENSO variability. The area with positive axis 2 scores ("coastal tropical" habitat) is small in 1986 and slightly reduced in 1987, increases in 1988 and remains almost as large in 1989. Whitebelly spinners were seen almost exclusively in waters with positive axis 2 scores, as represented

in the ordination diagram (Fig. 5). Eastern spinners ranged throughout both positive and negative areas. They were not closely associated with this axis (Fig. 5) but seemed to be found in the eastern (more coastal) part of the warm tropical habitat defined by negative axis 1 scores.

DISCUSSION

The ordination results were generally consistent with past studies of ETP cetacean ecology. The placement of common dolphins and blue whales into "cool upwelling" habitat is consistent with results reported by Au & Perryman (1985), Reilly (1990) and Reilly & Thayer (1990). The placement of spotted and spinner dolphins in contrasting habitat (essentially warm tropical water) is also as reported earlier. Consistency with results of Reilly (1990) is not surprising, because that study shared data from 1986 and 1987 with this study, but is somewhat reassuring because different analytical techniques were used.

The second axis successfully separated eastern spinners co-schooled with spotted dolphins from whitebelly spinners co-schooled with spotted dolphins. The placement of whitebelly spinners in habitat with a deeper thermocline follows from their more offshore distribution and the general tendency for the thermocline to shoal to the east in the ETP. Spotted dolphins alone (and eastern spinners alone) were placed intermediate to these mixed schools. If this is a general pattern it suggests that the two mixed spotted & spinner school types are utilizing habitats as different as those used by separate species (e.g. common dolphins and spotted dolphins on axis 1). The second axis also separates blue from Bryde's whales. These are the predominant baleen whale species of the ETP (e.g. Leatherwood et al. 1982), with other species only rarely occurring in the region.

The environmental patterns represented in the CCA axes are very similar to simple ordinations made by principal components analysis (PCA). For example, site scores of the first component of a PCA of TEMP, SAL, Z20 and LOGC for 1986 (Fig. 8) display spatial patterns quite close to those from the first CCA axis for that year (Fig. 6a). This shows that ETP cetaceans are responding to the major components of environmental variation, and allows straightforward interpretation of environmental processes represented by the CCA axes. The linear combinations of environmental variables extracted by CCA are in fact weighted principal components, the weights being functions of the species data (Ter Braak 1987). If we can interpret habitats defined by CCA as ecological niches, this result suggests that ETP cetaceans are exhibiting partial niche separation along the longest axes of environmental variability.

The maps are inherently less precise representations of

species-environment patterns than data analyzed in CCA for two reasons. First, the maps show only presence-absence, while we used an effort-corrected index of abundance (daily encounter rate) in the CCA. Second, the contouring requires some smoothing and interpolation between sites, while the CCA compared abundance indices only to environmental variables measured during the same day, along the same track lines where the cetaceans were sighted. This also accounts for the apparent disparity between error bars on ordination diagram (Fig. 5b) and the maps. For example, the 95% confidence limits for spotted (all categories) and common dolphins have only slight overlap on axis 1, while in Fig. 6 the spatial overlap of sightings appears more prominent. These species are apparently separating more strongly on a smaller scale than we could effectively represent on the maps.

One important result of the CCA was that all significant interannual variation in the species data was effectively accounted for by interannual variation in the environment. This was clearly demonstrated by the very low eigenvalue ($\lambda = 0.03$, $P = 0.21$) for interannual differences after extracting variance associated with the four oceanographic variables. This result does not apply to total population abundances, however, since we did not include group size estimates in our species data.

The species-environment variation extracted by the canonical correspondence analysis accounted for 42% of the total encounter rate variance. This is quite good given the unknown but surely large sampling variability inherent in daily encounter rates as an index of abundance for something so patchily distributed as cetacean schools. In linear methods (such as canonical correlation, the linear counterpart to CCA) all eigenvalues would sum to 1.0 making interpretation easier, but the R^2 also would be lower, due to mismatch of the linear model to modal distributions. An indirect " R^2 " evaluation had to be used with CCA, and it provides only an approximate result.

We suggest two approaches to use the results of this study in trend monitoring for ETP cetaceans. Other, perhaps more sophisticated approaches are possible. We present these only as examples. The most straightforward approach, involving minimal assumptions, would be to post-stratify the data for each year separately, based on the spatial distribution of CCA axis scores and the weighted mean and sd of those scores for the species of interest. Species/stocks that have similar means and sd's could use common strata. For example, separate strata could be defined using axis 1 for common and spotted dolphins. Axis 2 could be used to provide strata for whitebelly spinner dolphins. Because we have probability distributions for the occurrence of these species along the canonical axes, we would not be limited to use just two strata but could use three or four. After the data were stratified based on the species annual habitat distributions, standard line transect methodology would be followed. This is generically similar to the

post-stratification approach taken by Anganuzzi & Buckland (1989) to reduce bias in estimates of dolphin abundance from tuna vessel observer data.

A second possible approach would quantify the amount of habitat available within the study area each year, for each species/stock. The simplest quantification scheme would define only two strata for each. The cut-point between strata could be the 95% limit of the species/stock's distribution on the axis, or, less conservatively, the appropriate upper or lower quartile. More complex schemes using more than two strata could be developed, as with the post-stratification, based on additional information in the species probability distributions. The amount of any stratum available in a year could be quantified by, say, lightly smoothing and interpolating the CCA site scores (to provide values for all locations) and "sampling" the distribution with the actual cruise tracks for the year. If for example common dolphin habitat was to be defined as axis 1 > [some value], the amount of ocean sampled with axis 1 > [some value] in 1986 could be scaled as 1.0. The amount sampled in subsequent years could be scaled to the 1986 amount. The result would be a vector of values representing the amount of common dolphin habitat available within the ETP by year. This vector could then be applied to the encounter rate portion of the line transect abundance estimate for each year to account for changing availability of common dolphin habitat. If interannual differences were subsequently observed in the line transect abundance estimates, we could be more confident that they represent real changes in abundance, rather than just apparent changes due to spatial redistribution relative to sampling effort following habitat shifts.

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APPENDIX. Summary of models and algorithm used in canonical correspondence analysis, from Ter Braak (1986).

Notation

Y_{ik}	is the abundance of speices/stock k at site i
Y_{+k}	is the total abundance for species k ($k=1,m$)
Y_{i+}	is the total abundance of all species at site i ($i=1,n$)
x_i	is the site score for i from the species data
x_i^*	is the score for site i from the environmental data
$\mathbf{x}$	is a column vector of the x_i
$\mathbf{x}^*$	is a column vector of the x_i^*
λ	is the eigenvalue of the ordination axis
μ_k	is the weighted mean for species k
$\mathbf{b}$	is a column vector of regression coefficients
$\mathbf{R}$	is a diagonal $n \times n$ matrix with Y_{i+} as the (i,i) -th element
$\mathbf{Z}$	is an $n \times (q+1)$ matrix containing the environmental data and a column of ones

Transition Formulae of CCA

$$\lambda \mu_k = \sum_i Y_{ik} x_i / Y_{+k} \quad (1)$$

$$x_i^* = \sum_k Y_{ik} \mu_k / Y_{i+} \quad (2)$$

$$\mathbf{b} = (\mathbf{Z}'\mathbf{R}\mathbf{Z})^{-1} \mathbf{Z}'\mathbf{R}\mathbf{x}^* \quad (3)$$

$$\mathbf{x} = \mathbf{Z}\mathbf{b} \quad (4)$$

Algorithm of CCA

- Step 1. Start with arbitrary but unequal site scores (x_i);
- Step 2. Calculate species scores (μ) by weighted averaging of site scores (Eq. 1);
- Step 3. Calculate new site scores (x_i^*) by weighted averaging of species scores (Eq. 2);
- Step 4. Obtain regression (canonical) coefficients by weighted multiple regression of the site scores on the environmental variables (Eq. 3). The weights are the site totals (Y_{i+}).
- Step 5. Calculate new site scores (Eq. 4); center and standardize them ($\sum_i Y_{i+} x_i = 0$ and $\sum_i Y_{i+} x_i^2 = 1$);
- Step 6. Stop when new site scores sufficiently close to previous iteration, otherwise go to Step 2.

Table 1. Search effort and number of cetacean schools recorded by year, 1986 - 1989, from the Monitoring of Porpoise Stocks expedition in the eastern tropical Pacific.

	1986	1987	1988	1989	Total
Km Searched	<u>28,693</u>	<u>28,175</u>	<u>25,160</u>	<u>28,860</u>	<u>118,907</u>
No. sightings of					
spotted dolphins	80	91	45	80	296
common dolphins	51	32	72	57	212
spotted with eastern spinner	44	39	33	49	165
spotted with whitebelly spin.	32	29	23	23	107
eastern spinner	28	18	6	19	71
whitebelly spinner	8	10	18	8	44
striped	154	183	202	212	751
rough-toothed dolphin	32	25	39	37	133
bottlenose dolphin	91	80	62	67	300
pilot whale	43	49	54	58	204
pilot with bottlenose	15	18	22	21	76
Risso's dolphin	38	62	44	46	190
sperm whale	99	63	48	76	286
blue whale	5	5	6	11	27
Bryde's whale	7	8	9	13	37
unid. baleen whale	46	64	63	64	237
Totals	773	776	746	841	3,136

Table 2. Oceanographic data from the Monitoring of Porpoise Stocks expedition, 1986-1989, used in the canonical correspondence analyses.

	<u>1986</u>	<u>1987</u>	<u>1988</u>	<u>1989</u>	<u>Total</u>
km Surface Temperature, Salinity	28,693	28,175	25,160	28,860	118,907
Surface Chlorophyll Measurements	3,763	1,927	3,613	3,552	12,855
XBT Measurements	1,144	1,160	835	778	3,917
CTD Measurements	244	280	352	352	1,228

Table 3. Correlation coefficients among environmental variables, canonical species axes and environmental axes estimated by a canonical correspondence analysis of cetaceans in the eastern tropical Pacific during 1986 - 1989. Values marked with an * are significantly different from zero at $\alpha \leq .05$.

	SPEC AX1	SPEC AX2	SPEC AX3	SPEC AX4	ENVI AX1	ENVI AX2	ENVI AX3	ENVI AX4	TEMP	SAL	LOGC	Z20
SPEC AX1	1.0000											
SPEC AX2	-.0118	1.0000										
SPEC AX3	.0026	.0356	1.0000									
SPEC AX4	-.0281	.0728	-.0288	1.0000								
ENVI AX1	.6422*	.0000	.0000	-.0001	1.0000							
ENVI AX2	.0000	.4461*	.0000	.0000	.0000	1.0000						
ENVI AX3	.0000	.0000	.2598*	.0000	.0000	.0000	1.0000					
ENVI AX4	.0000	.0000	.0000	.1799	.0000	.0000	.0000	1.0000				
TEMP	-.6003*	-.0976	.0725	.0029	-.9349*	-.2187	.2791*	.0158	1.0000			
SAL	.0940	.1414	-.2393*	-.0310	.1464	.3170*	-.9211*	-.1721	-.4660*	1.0000		
LOGC	.3161*	-.1779	.0117	-.1390	.4922*	-.3988*	.0451	-.7724*	-.3726*	.0370	1.0000	
Z20	-.3462*	.3623*	.0463	-.0243	-.5391*	.8120*	.1781	-.1351	.3739*	.0377	-.4768*	1.0000

Table 4. Canonical eigenvalues from a CCA of cetacean abundance and oceanographic conditions in the eastern tropical Pacific during August - November 1986 - 1989. % S-E is the cumulative percent of the species - environment variance accounted for by each axis, % total is the cumulative percent of the total variance in cetacean abundance accounted for. P-values are from a Monte Carlo randomization test.

Axis	Eigenvalue	% S-E	% total	P-value
1	0.201	66.6	27.6	<.01
2	0.077	92.0	38.1	
3	0.015	97.1	40.2	
4	0.009	100.0	41.6	
Trace (S-E)	0.301	100.0	41.6	<.01
(Interannual	0.030	0.0		.21)
Residual	0.428	0.0	58.7	<.01
Total	0.729		100.0	

Figure 1. Dolphin distributions in the northern summer in the eastern tropical Pacific, from Reilly (1990). Contours are for encounter rates per 185 km searched. Dots represent centers of 2° squares in which there was at least 185 km search effort.

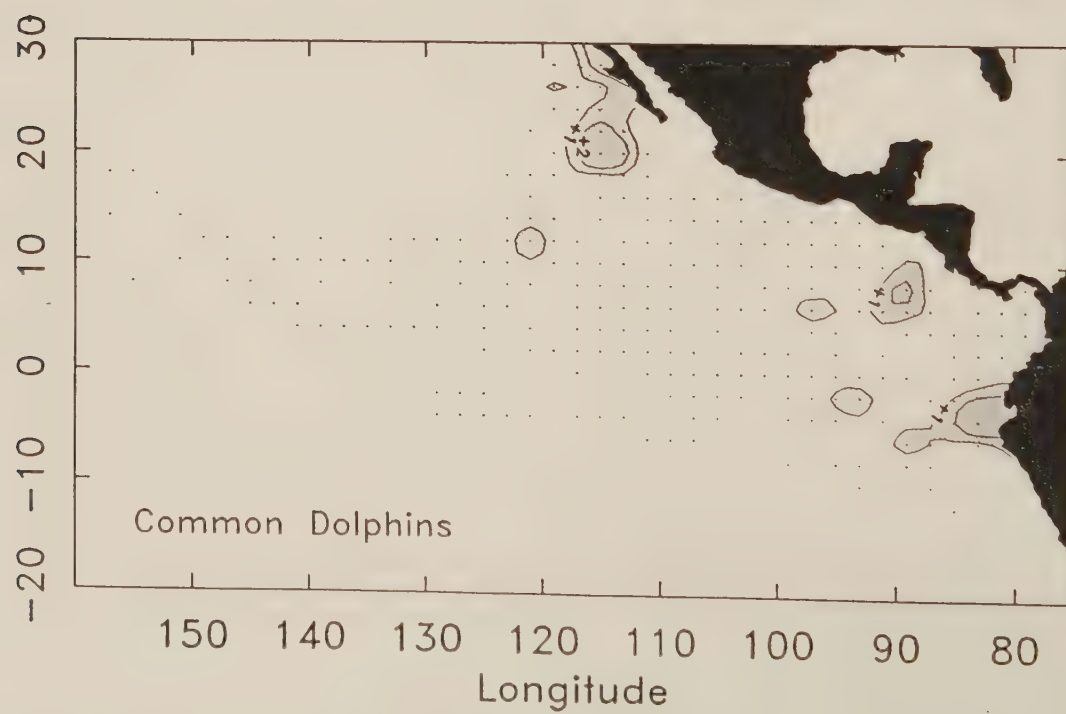
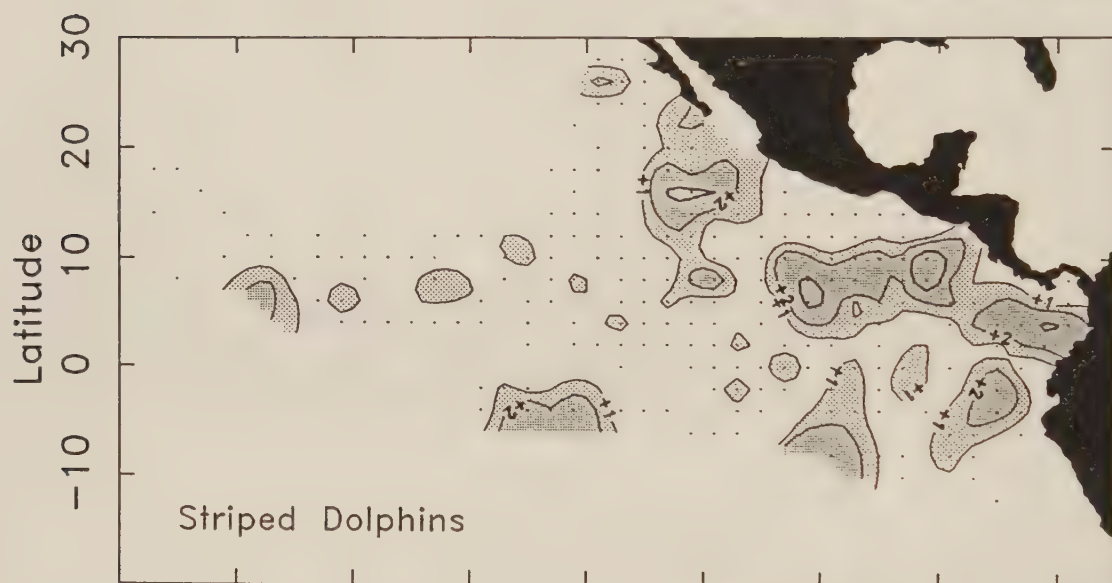
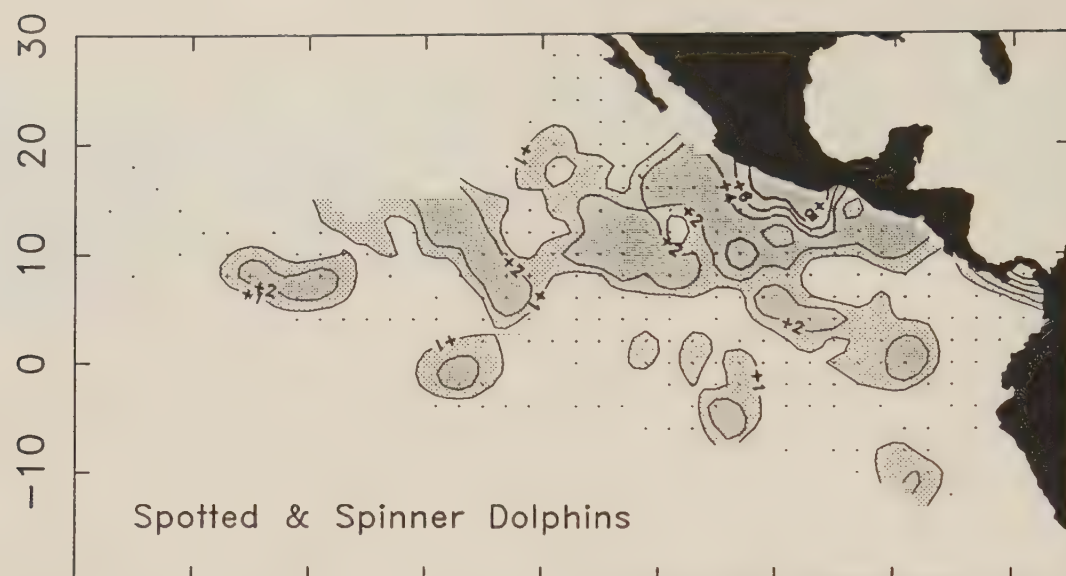


Figure 2. Schematic representation of the surface circulation and water masses of the eastern tropical Pacific.

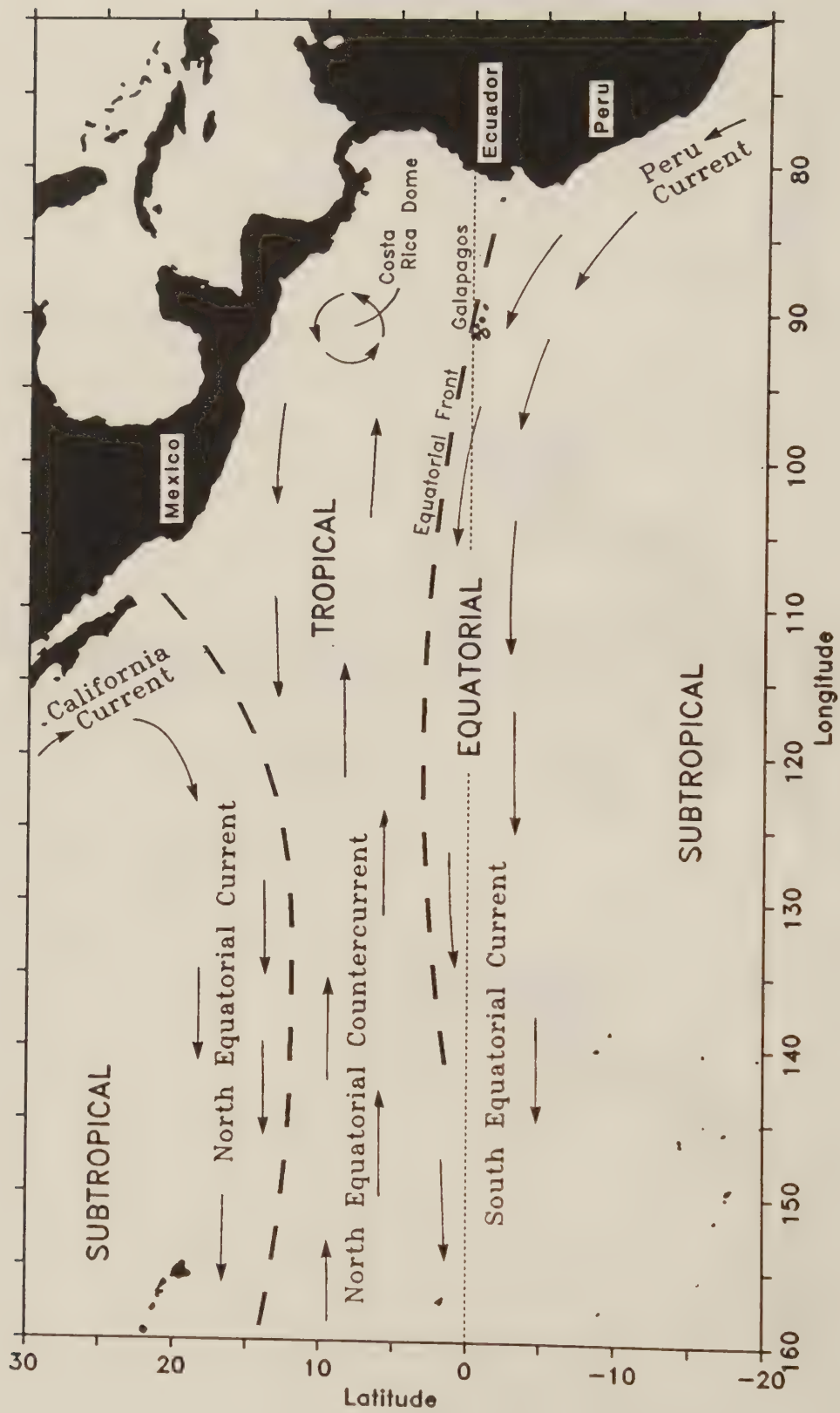


Figure 3. Cruise tracks of R/V David Starr Jordan and McArthur during August - November, 1986 - 1989.

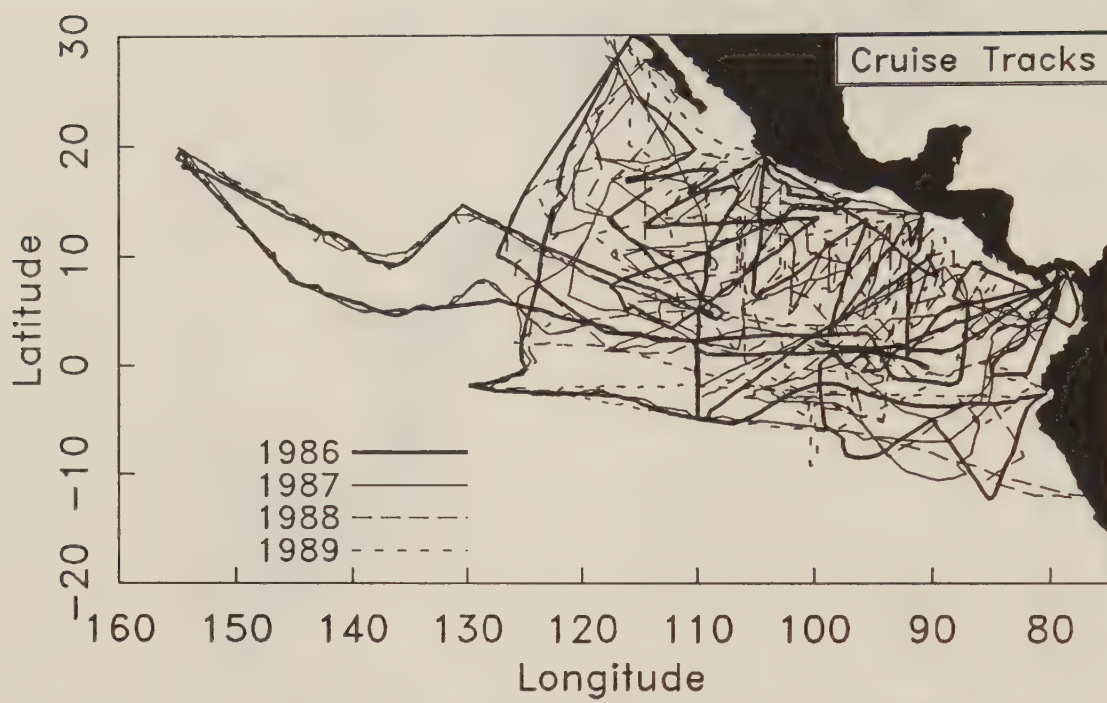
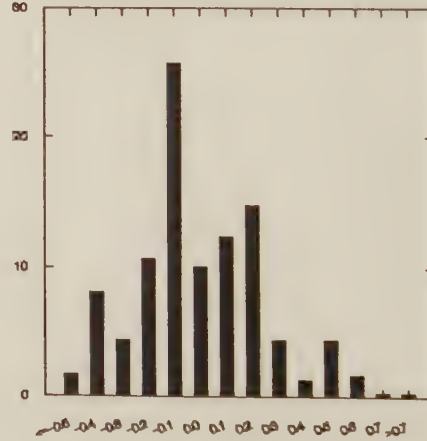
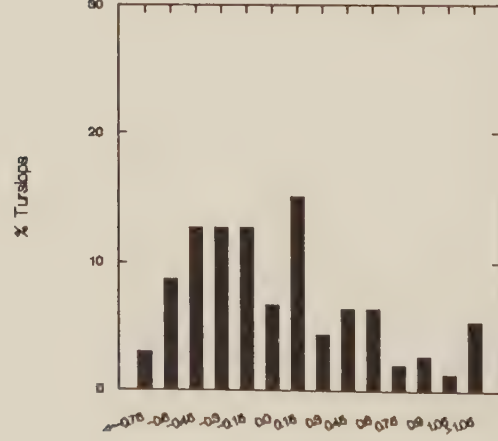
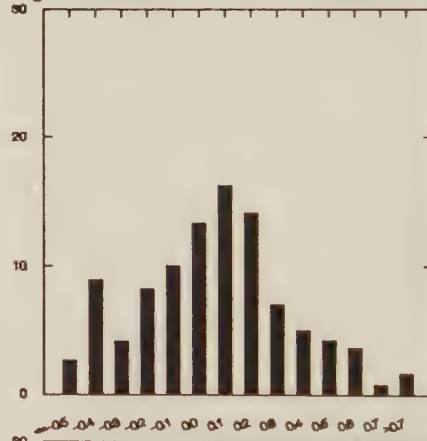
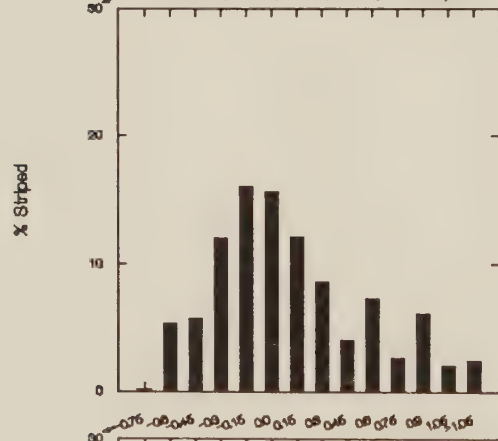
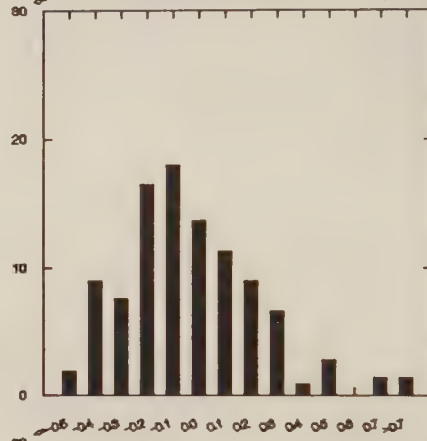
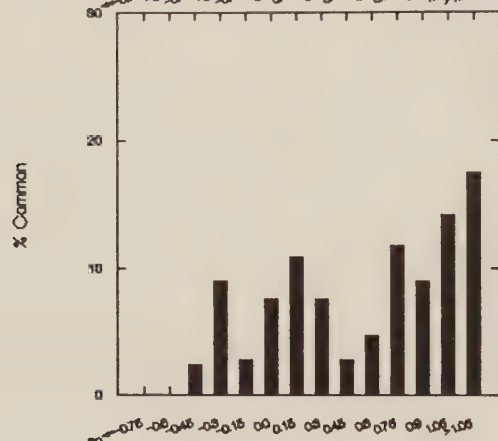
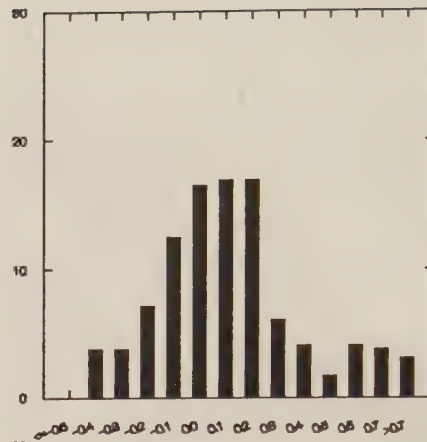
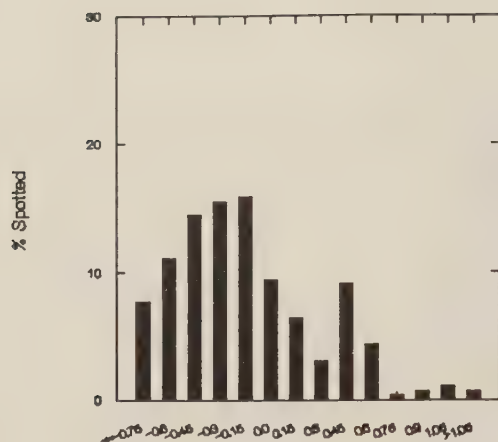
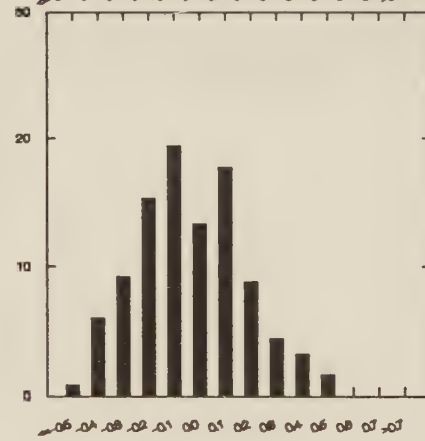
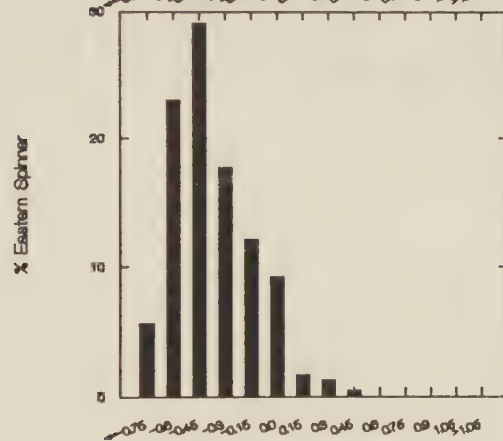
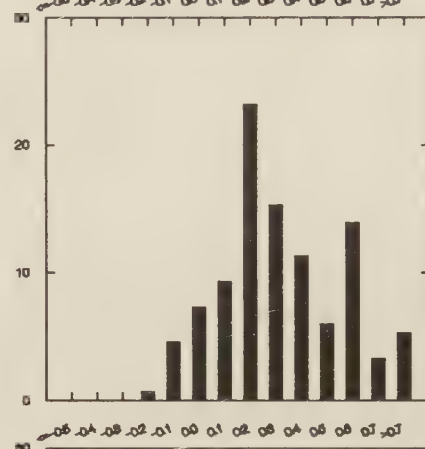
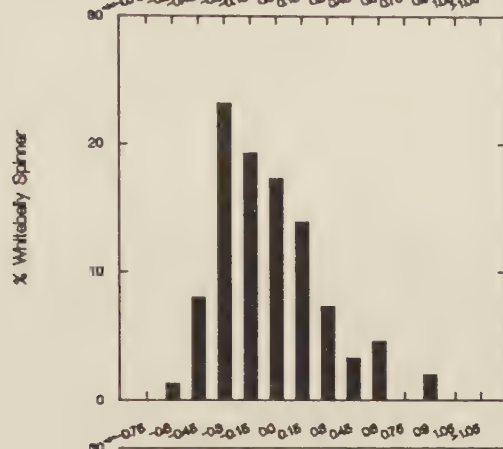
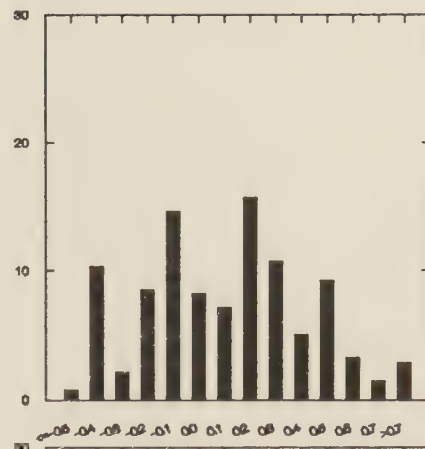
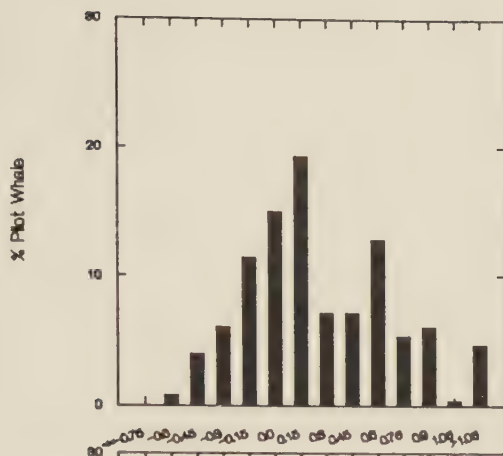


Figure 4. Frequency histograms, transformed to percentages, of the first two environmental axis scores in areas where cetaceans were sighted for 7 species/stocks.



Canonical Axis 1

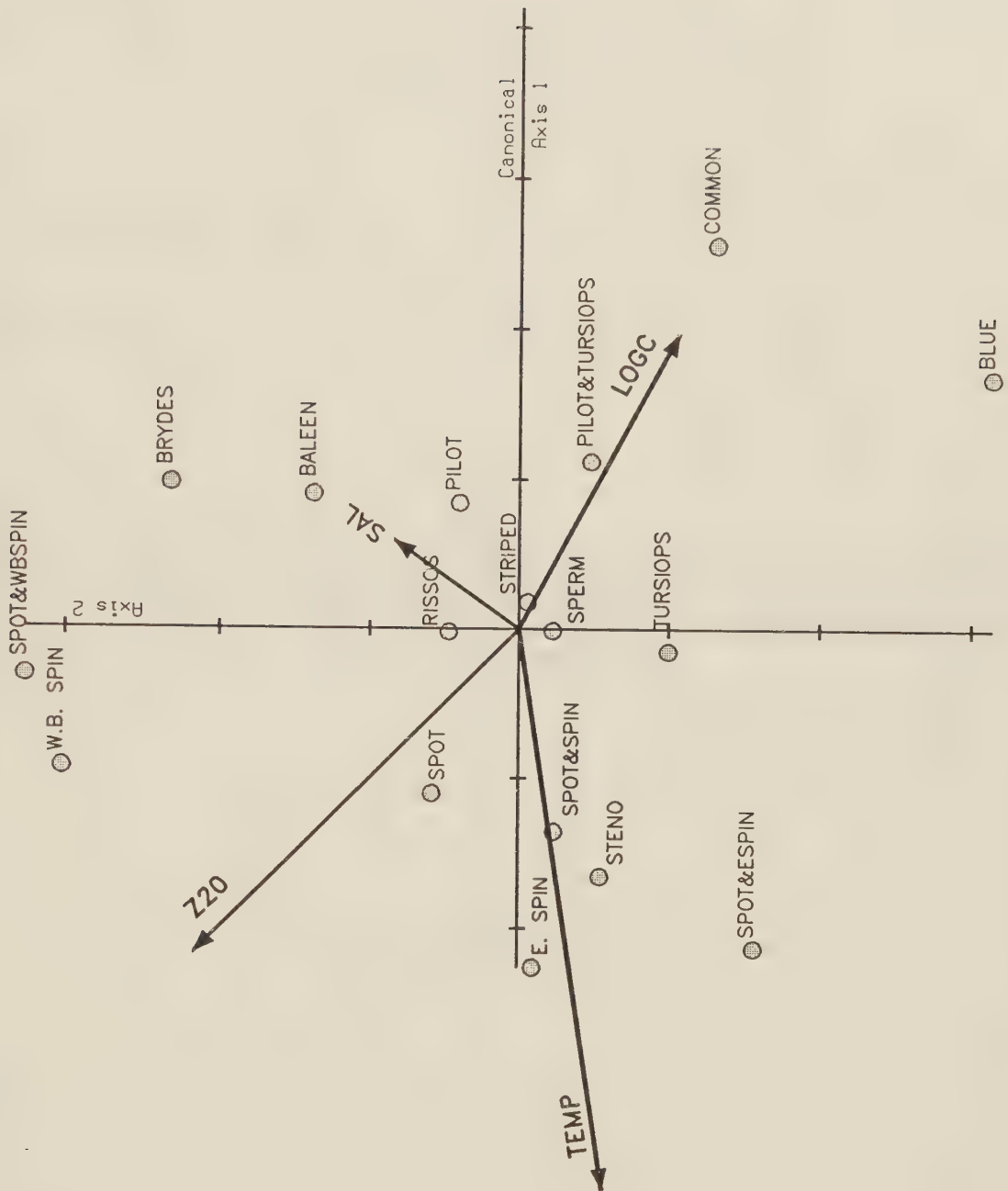
Canonical Axis 2



Canonical Axis 1

Canonical Axis 2

Figure 5. Ordination results from canonical correspondence analysis of cetacean species/stocks and environmental conditions in the eastern tropical Pacific. (a) Biplot of first two species canonical axes and environmental variables. (b) Ordination showing 95% confidence limits of selected species. The environmental variables, represented by arrows, are: surface temperature (TEMP), surface salinity (SAL), thermocline depth indexed by 20°C isotherm depth (Z20), and surface chlorophyll, log-transformed (LOGC). These two axes represent 92% of the species-environment variance, 42% of the total encounter rate variance.



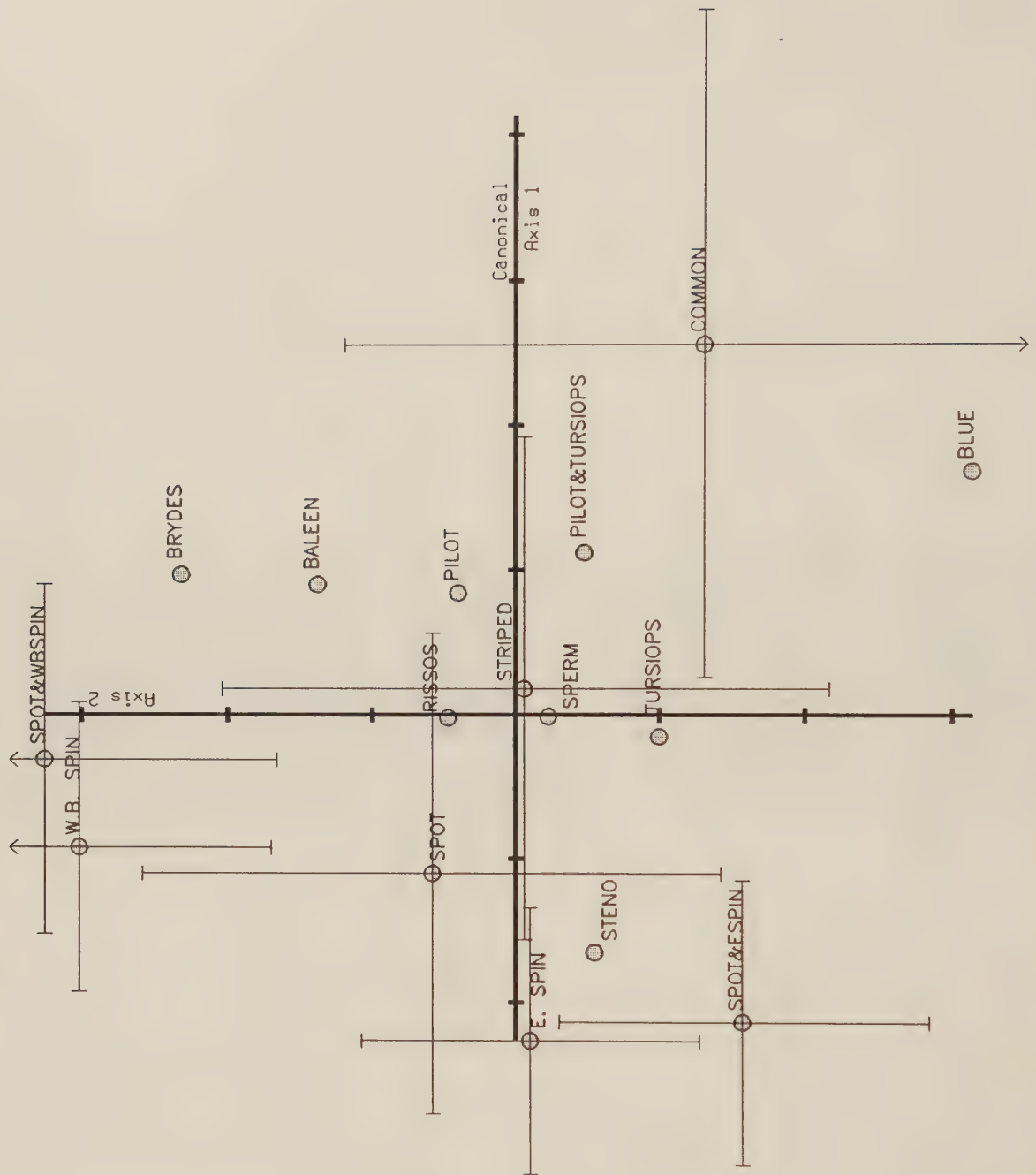
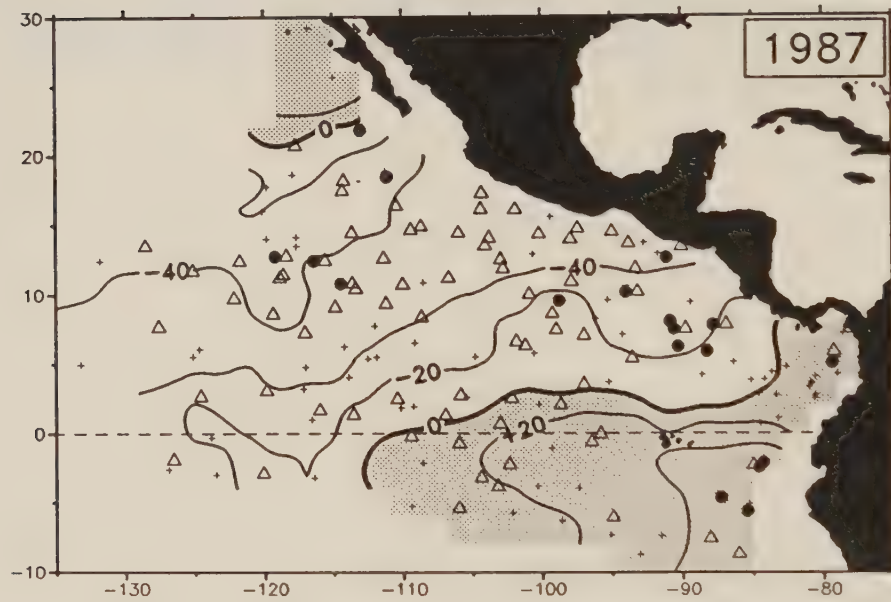
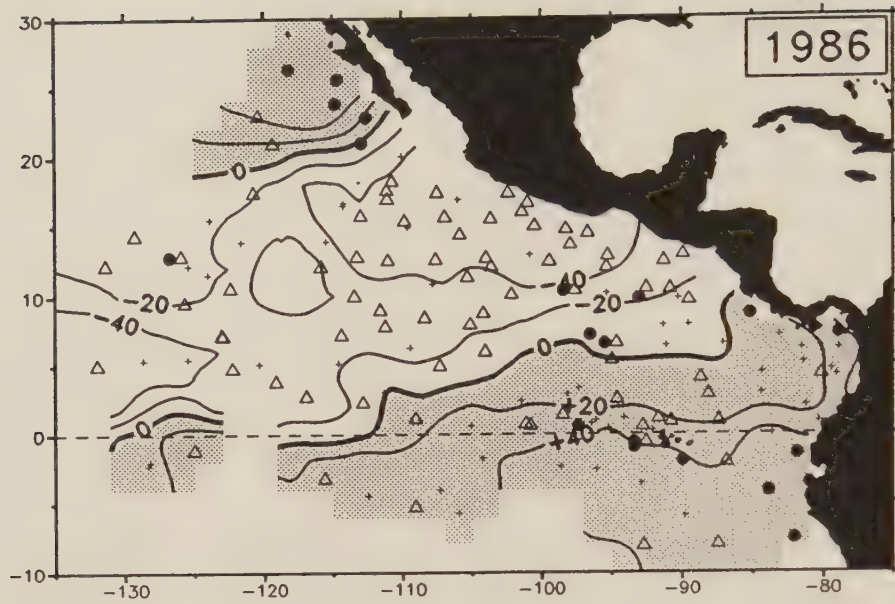


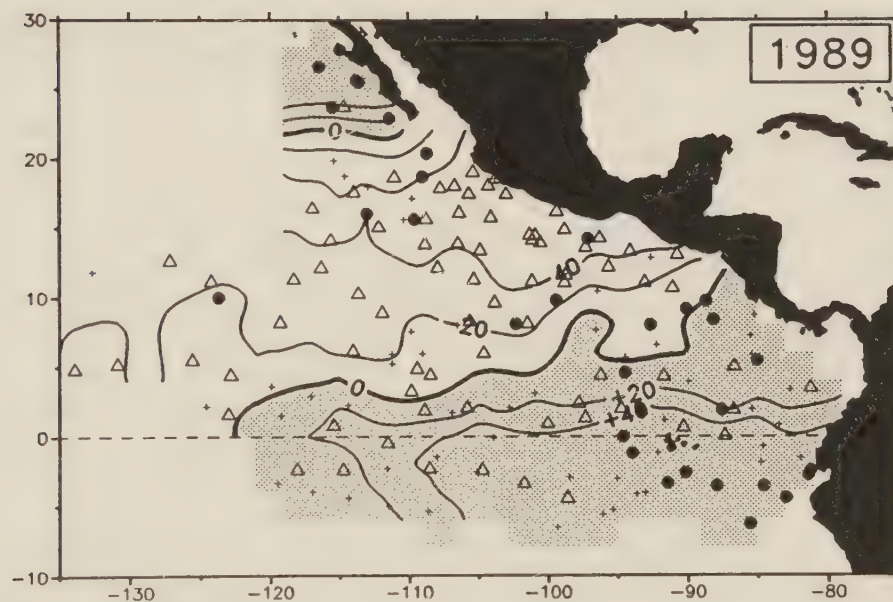
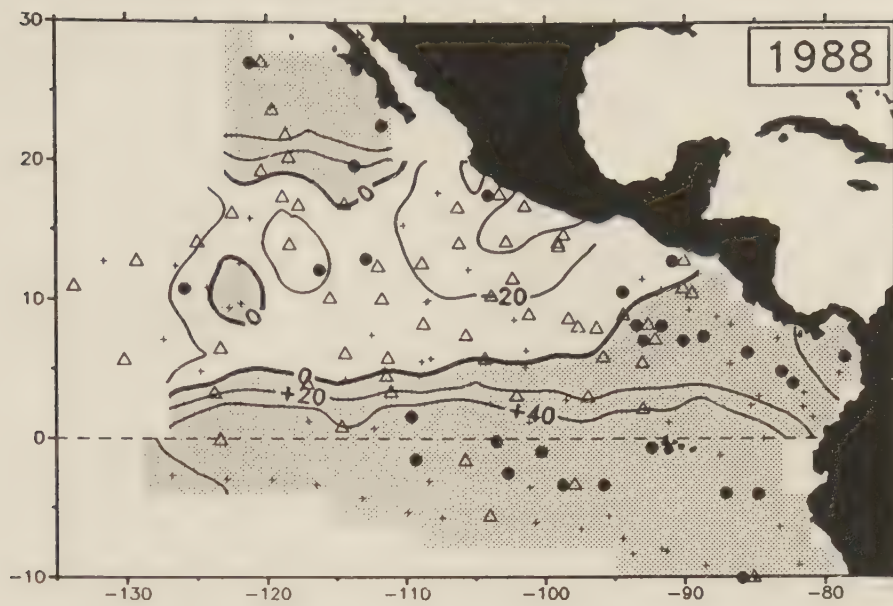
Figure 6. Maps of distribution of canonical axis 1 for 1986-1989. Positive areas are shaded. Spotted dolphin sighting localities are shown as open triangles, common dolphin localities as closed circles. A "+" represents a sighting day during which neither spotted nor common dolphins were seen.

CANONICAL AXIS 1



● Common dolphin △ Spotted dolphin

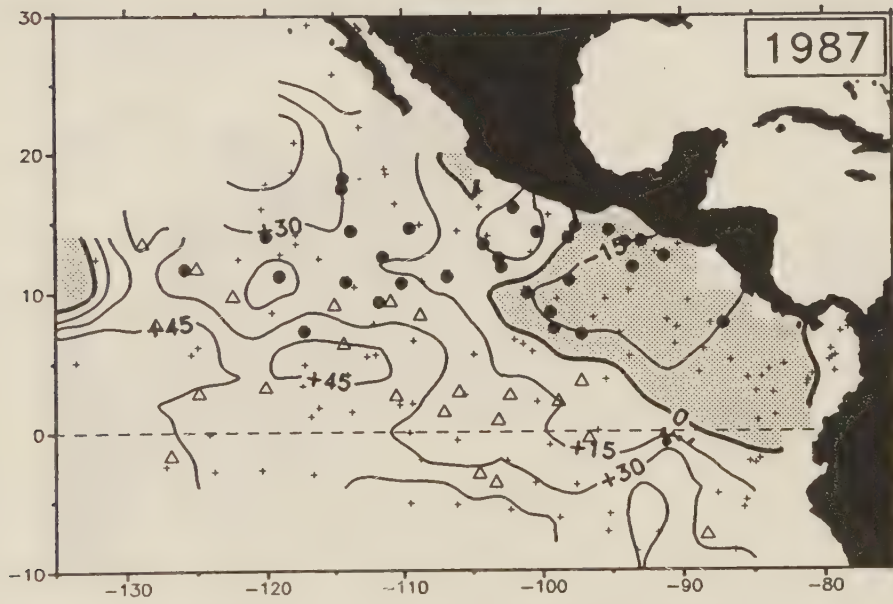
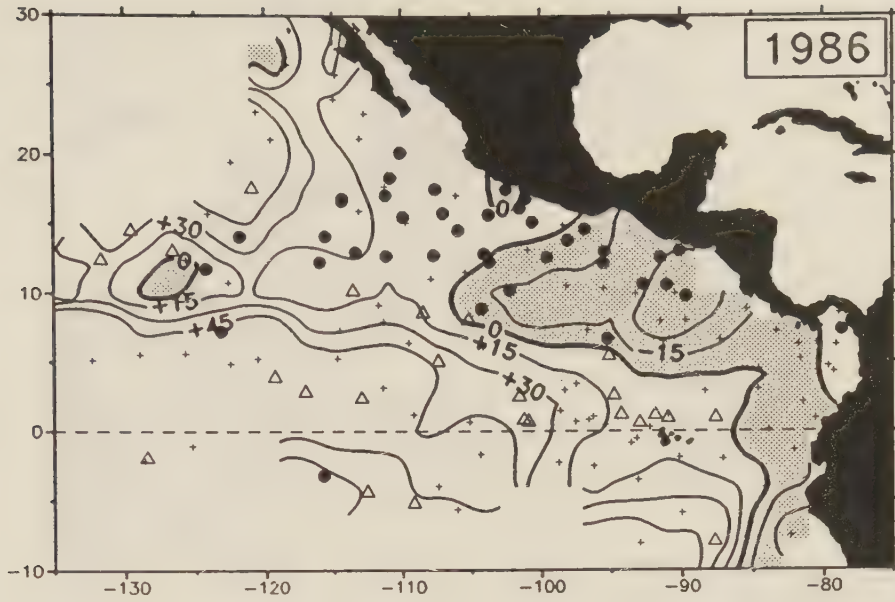
CANONICAL AXIS 1



● Common dolphin △ Spotted dolphin

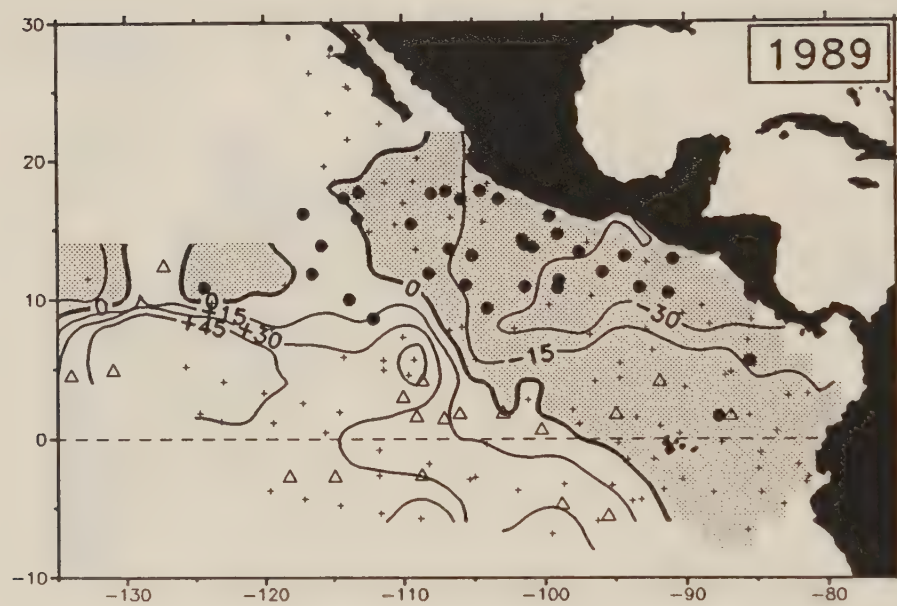
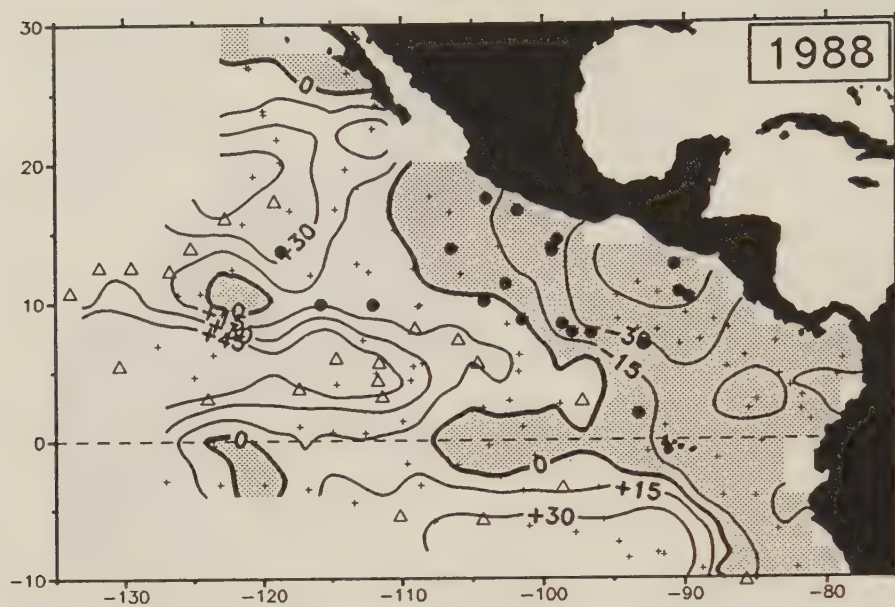
Figure 7. Maps of distribution of canonical axis 2 for 1986-1989. Negative areas are shaded. Eastern spinner sighting localities are represented by closed circles, whitebelly spinner localities by open triangles.

CANONICAL AXIS 2



● Eastern Spinner △ Whitebelly Spinner

CANONICAL AXIS 2



• Eastern Spinner Δ Whitebelly Spinner

Figure 8. Maps of distribution of principal component 1 from environmental data collected during 1986-1989, for comparison to CCA axis 1 shown in Fig. 6.

PRINCIPAL COMPONENT 1

